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A description of the growth of sheep and its genetic analysis

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Abstract

The Gompertz is one of a family of growth functions that, when the environment (e.g. food, housing) is non-limiting, provides a useful description of growth as a comparatively simple, single equation. It has three parameters of which the important ones are mature size, A*, and the rate parameter,* B*. Estimates of* A *and* B*, however, are highly correlated and defining their separate values for individual animals is problematic. This problem was explored using five methods for estimating the parameters, or transformations of them, to describe the growth of two genotypes of Suffolk sheep kept under non-limiting conditions. One genotype was under selection for high lean growth rate and the other was its control. Live weights that were collected at least fortnightly from near birth to 150 days of age over a 9-year period on 1934 lambs were used. The Gompertz form adequately described the growth of the great majority of the lambs evaluated. When considering* A *and* B *as a lumped parameter,* Z = A·B*, and fitting* Z*,* B *and an initial condition (a transformed birth weight) as the parameters, the problems in estimation were substantially overcome as shown by a low correlation of* Z *with estimates of* B *both within and across animals. Usefully* Z *has a biological interpretation in that* Z/e *is the maximum daily growth rate. Since the Gompertz form adequately described growth in these sheep, the extent of genetic co-variation for the growth parameters values (*A*,* B*,* Z*) was estimated to determine if they were amenable to selection. A weighted univariate animal model was fitted. Mature size,* A*, and the rate parameter,* B*, were moderately heritable (0·37 (s.e. 0·04) and 0·38 (s.e. 0·05), respectively) as was live weight at 150 days of age (0·31 (s.e. 0·06)). However there was a substantial negative genetic relationship between* A *and* B *(−0·48).* Z *was highly heritable (0·72 (s.e. 0·05)). After 9 years of selection, the genotype selected for high lean growth rate was heavier (*P < 0·001*) at 150 days of age (5·2 kg) and at maturity (6·6 kg), with a maximum growth rate (*Z/e*) that was 1·12 times that of the control. Our lumped parameter* Z*, in effect a rate parameter scaled for mature size, avoided problems in estimating* A *and* B *and, in so doing, offers a general and robust description of lamb growth amenable to selection.*

Keywords: *genetic parameters, Gompertz function, growth, sheep.*

Introduction

The idea that an animal of a given kind will grow to a final or mature size is both widely accepted and useful (Brody, 1945; Parks, 1982). The question of the scale on which size is best measured remains open, at least as far as sheep are concerned. In models of pig and poultry growth it has been found to be useful to express mature size in terms of protein weight (Emmans and Fisher, 1986; Knap, 2000). With the protein content of the mature lipid-free empty body being essentially constant (Emmans, 1988), the use of protein as the measure of mature size is equivalent to defining mature size as the mature lipid-free empty body weight. As the empty body weight is the sum of the lipid-free and lipid weights, the use of this scale allows mature size and mature fatness to be treated as separate characteristics. Taylor *et al.* (1986) proposed that mature size should be expressed as the observed mature weight adjusted to a constant level of fat content of 25%. With lipid-free weight as a measure of mature size this is equivalent to following the suggestion of Taylor *et al.* (1986) but

with the 'constant level of fat' set at 0%. The latter adjustment makes it easier to distinguish between the separate ideas of mature size and mature fatness.

While in terms of modelling there are advantages in constructing the body from the weight of its components, there is the disadvantage that the amount of information from slaughter experiments in which body composition is measured is much scarcer, and more expensive to obtain, than data on live weight. Also, as accurate measures of weight can be obtained repeatedly for a given animal, it is sensible to start with ideas about such live weight data in order to make the first steps towards a growth model. The power of the approach will be greater as the range, and to a lesser extent, the number of observations increases. These steps are made here for sheep. Similar analyses have been done for poultry (Emmans and Fisher, 1986; Hancock *et al.*, 1995; Gous *et al.*, 1999) and pigs (Knap, 2000).

There are many forms of equations that have been proposed to describe growth (Winsor, 1932; Parks, 1982; France *et al.*, 1996). The criteria used to decide among them also differ. In this study, our approach was to choose a form of an equation which had the main properties expected, which had few parameters and which had support from at least some data sets. The desired properties of a growth function are (i) weight tends to a final or asymptotic value with time, (ii) growth rate has a maximum at some intermediate weight, and (iii) the relative growth rate decreases monotonically, preferably in some simple way, as weight increases toward maturity. A growth equation with these properties, although not the only one, is the Gompertz function which benefits from having only three parameters, of which two are the important ones and the other the initial condition. This function has been, and is being, widely used for describing a variety of material. Among the recent uses are the following. Admassu and Ahlgren (2000) used it to describe the growth in length of fish, as did Akbas and Yaylak (2000) for growth in Japanese quail. Arseneau *et al.* (1998) used the function to assess the relationship between time since lichen colonization and standing lichen biomass. It was used by Clark *et al.* (2000) for the growth of whales, by Gous *et al.* (1999) and Mignon-Grasteau *et al.* (2000) for chickens, and by Friggens *et al.* (1997) and Zygoyiannis (1997) for sheep. Bajzer (1999) has discussed possible reasons for the function being a good description of growth. As there is support for it being a useful and robust description of the potential of an animal to grow we chose the Gompertz form to describe growth in this study.

The Gompertz, or any other growth function, cannot be expected to describe all actual growth curves. Whether by accident or design, animals do not always achieve their potential to grow. The failure may be due to inadequate feeding, disease or adverse environments, including the climatic environment. A consequence is that real growth data tend not to be properly described by a smooth function with the same values of the parameters throughout. The data may have discontinuities or changes arising from environments which cause a variable deviation from the potential. But there are cases where the potential to grow is met at most if not all times and in such cases the data are expected to be well described by the function (Emmans, 1997).

The main objective of this study was to explore the use of the Gompertz equation in describing the actual growth of two genotypes of Suffolk sheep kept under environmental conditions designed to be non-limiting. In doing so, we consider the considerable problems in estimation when fitting this function to data from individual animals. If the parameters of the Gompertz form adequately describe the potential growth of an animal, then variation between animals in the values of those parameters may be, in part, genetic in origin. Thus, as the final aspect of this study, the extent of genetic co-variation for the values of the parameters of the Gompertz form are estimated.

Material and methods

Gompertz growth function

The Gompertz growth function arises from the assumption that relative growth rate, $(dW/dt)/W$, declines linearly with the weight of an animal on a logarithmic scale. That is

$$(dW/dt)/W = a - B \cdot \ln W \qquad (1)$$

where W is live weight, t is time and B is a rate parameter. Since the relative growth rate will be zero when $W = A$, the mature size, then

$$0 = a - B \cdot \ln A \qquad (2)$$

which leads to $a = B \cdot \ln A$. By substituting into equation (1)

$$(dW/dt)/W = B \cdot \ln A - B \cdot \ln W \qquad (3)$$

which can be written as

$$(dW/dt)/W = B \cdot \ln(A/W) \qquad (4).$$

The absolute growth rate (dW/dt) is then

$$dW/dt = B \cdot W \cdot \ln(A/W) \quad (5).$$

When equation 5 is divided through by mature weight A, it becomes

$$du/dt = B \cdot \ln(1/u) \quad (5a)$$

where the degree of maturity in weight, u, is defined as $u = W/A$ and du/dt is the rate of maturing. The form of equation (5a) is in Figure 1 and shows that the rate of maturing has a maximum when $u = 1/e \approx 0{\cdot}368$. The only parameter that affects the rate of maturing is B, as shown in Figure 1. On integration, equation (5) leads to

$$W = A \cdot \exp(-\exp(G_0 - B \cdot t)) \quad (6)$$

where the third parameter, G_0, is a transformed initial weight given by $G_0 = \ln(-\ln(W_0/A))$ and W_0 is the weight at $t = 0$. Integrating equation (5a) leads to the equivalent maturing curve

$$u = \exp(-\exp(G_0 - B \cdot t)) \quad (6a).$$

Methods for estimating the values of the growth parameters

Non-linear methods. In principle, the values of the three parameters of the Gompertz form can be estimated by fitting equation (6) to W, t data pairs (method Ia) using non-linear regression (Hancock *et al.*, 1995; Gous *et al.*, 1999). Where the range in W is as wide as the 4 kg near birth to the 80 kg at 150 days of age, a ratio of 20, as seen in this study, the use of the logarithmically transformed form of equation (6) which is:

$$\ln W = \ln A - \exp(G_0 - B \cdot t) \quad (7)$$

would be expected to be more suitable when the variances are roughly proportional to the values of W (method II).

Lewis *et al.* (1998) found that the estimates of A and B were very highly correlated. A possible way to overcome the inevitable problem of estimating A and B as separate parameters is to consider them together by defining a variable Z as the product $A \cdot B$. This lumped parameter Z would be expected to have a lower error of estimation, and a distribution of values closer to normal, than A and B separately and can be estimated (method Ib) from a modified form of equation (6) as

$$W = (Z/B) \cdot \exp(-\exp(G_0 - B \cdot t)) \quad (8).$$

Z has a biological interpretation in that Z/e is the maximum daily growth rate.

Linear methods. An alternative approach for estimation proposed by Emmans (1988) and Ferguson and Gous (1993a and b), is to use equation (1) where $(dW/dt)/W$ is estimated for each of a range of weights (method III). The values of $(dW/dt)/W$ are then regressed on $\ln W$ for the different time periods. For this study, the time interval between weights was specified as at least 10 days. The work of Cullis and McGilchrist (1990) suggests that estimates of A and B obtained by this approach will be highly correlated.

Equation (6) can be transformed to

$$G = -G_0 + B \cdot t \quad (9)$$

where $G = -\ln(-\ln(W/A))$, using a prior estimate of A. Successive estimates of A can be tested for their ability to give the same estimate of B for early and late independent subsets of the data. For this study, data were separated as those before and after weaning, with the values of A tested up to 400 kg (method IV).

The parameters obtained by the five estimation methods described are shown in Table 1.

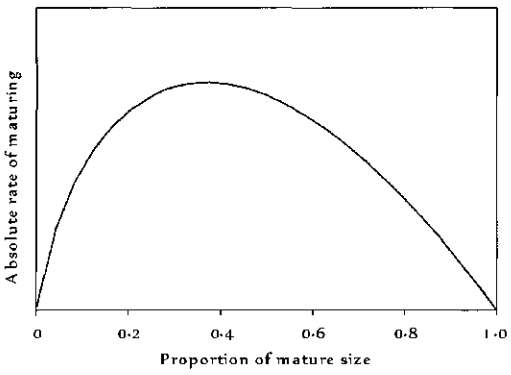

Figure 1 Rate of maturing (du/dt) relative to degree of maturity in weight, $u = W/A$, where t is time in days, W and A are live weight at time t and maturity, respectively (du/dt is by definition at its maximum when $u = 1/e \approx 0{\cdot}368$).

Sheep data

Suffolk selection flock. The data come from a selection experiment in Suffolk sheep at the Scottish Agricultural College (SAC) described in Simm *et al.* (2002). Between 1980 and 1983 about 160 mature Suffolk ewes were purchased by SAC, then the East of Scotland College of Agriculture, from 42 pedigree flocks throughout the United Kingdom. Lambing began in January. From a week of age, lambs were

Table 1 *Parameters estimated when using the five estimation methods*

Method	Fit	Description (equation†)	Growth parameters‡
Ia	Non-linear	Weight on time (6)	$A; B; G_0$
Ib	Non-linear	Weight on time (8)	$Z; B; G_0$
II	Non-linear	$\log_e$ weight on time (7)	$A; B; G_0$
III	Linear	Relative growth rate on $\log_e$ weight for period	$B_0; B$
IV	Linear	Iteration on prior estimate of A (9) for 2 periods	$A; B$

† Equation number as referenced in text.
‡ A is mature size, B is the rate parameter, G_0 is transformed initial weight ($\log_e(-\log_e(W_0/A))$), $Z = A - B$, and B_0 is the intercept of the regression of relative growth rate on $\log_e$ weight.

creep fed and gradually switched to a complete, pelleted diet that was high in energy and protein (12 MJ metabolizable energy and 180 g crude protein per kg dry matter). From weaning at 56 days of age, they were penned (in early years individually and in later years in groups) and offered this diet *ad libitum* until they were 6 to 8 months of age. The food was designed to allow each animal to fully express its genetic potential to grow.

At mating in 1985 a selection experiment began. The flock was closed and randomly divided into a selection and a control line; the selection line had about twice the number of the control. Firstly in ram lambs (from 1986), and latterly in ewe lambs (from 1989) as well, live weights (LWT), and ultrasound measurements of muscle (UMD) and fat depth (UFD), were recorded at 150 days of age. These measurements were combined into a selection index constructed as 0·103LWT + 0·257UMD − 0·406UFD. The index was designed to increase the rate of lean deposition, with little change in the rate of fat deposition (Simm and Dingwall, 1989). Lambs were selected on index score to produce one line with high index scores and another line with average index scores as the control. Index scores were scaled such that the average of the control line remained at 100 points, and the standard deviation of the index was 40 points.

The control line contained six sire families. In the selection line, six ram lambs with the highest index scores were chosen each year. No more than two sons of a sire were selected. In both lines, rams were used in their first year and for a single season.

The selection experiment ended in 1994. At that time response in live weight, and ultrasound muscle and fat depth, in both sexes amounted to between 7 and 15% of the overall mean of the trait (Simm *et al.*, 2002).

Live weights. Live weights were available on ram lambs from 1985, and on ewe lambs from 1989 through 1994. In 1985, 1986 and 1987 weights were collected about every 2 weeks from 56 (weaning) to generally 150 days of age (maximum age at weighing of 159 day). From 1988 onward weights were collected as often as weekly from near birth (as early as 2 days of age) through 150 days of age.

There were 2037 sheep with live weight records. Of these, 103 were excluded because they did not reach 150 days of age or were obviously ill for an extended period. The remaining 1934 sheep had in total 35401 live weights. Of these live weights, 63 were deleted as outliers (less than 0·2%). Outliers were defined as those with a standardized residual greater than 4·0 based on the linear regression of weight $j+1$ on weight j. Which of the pair of weights was removed as the outlier was determined by inspection. The remaining 35338 live weights gave an average of 18 (s.d. 5) observations for each animal.

Comparison of methods for obtaining growth parameters

The statistical characteristics of the values of the growth parameters obtained by different estimation methods were investigated using the non-parametric exploratory data techniques described by Ott (1993). With these techniques, values are identified by their distance from the median in relation to the inter-quartile range (IQR). The number of extreme observations was found for each growth parameter estimated by each of the five methods.

Four reasons for rejecting the total record of a sheep for inclusion in the genetic analysis were: (i) the iterative fit did not converge; (ii) the residual m.s. was $\geq 3{\cdot}5$ kg^2 for methods Ia and Ib, or the equivalent for method II; (iii) A was ≥ 300 kg; or, (iv) Z was $\geq 2{\cdot}4$ kg/ day. The rejection values chosen for the latter three criteria were based on the exploratory techniques described above. They correspond with a value 3·5 times the IQR above the median. There were no values this distance below the median. However for method III there were 10 estimates of A that were low (less than 20 kg) and these too were excluded.

Using these rejection criteria, an 'accepted set of sheep' was defined for each estimation method. For these, the shapes of the distribution of the growth parameter values were checked for skewness and

kurtosis using Genstat (Genstat 5 Committee, 1998). The relationships between parameter values were summarized, within each method, as (i) the correlation of the estimated values obtained within an animal, and (ii) the correlation of the estimated values across animals. The linear regression of each growth parameter between estimation methods was also fitted.

Linear mixed-model

A linear mixed model was defined as:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z_d d} + \mathbf{Z_m m} + \mathbf{Z_c c} + \mathbf{Z_r r} + \mathbf{e_e} \qquad (10)$$

to describe the set of accepted growth parameters values, where $\mathbf{y}$ was a vector of observations, $\mathbf{b}$ was a vector of fixed systematic environmental effects with incidence matrix $\mathbf{X}$, and $\mathbf{d}$, $\mathbf{m}$, $\mathbf{c}$ and $\mathbf{r}$ were vectors of random direct additive, maternal additive, litter and birth year effects with incidence matrices $\mathbf{Z_d}$, $\mathbf{Z_m}$, $\mathbf{Z_c}$ and $\mathbf{Z_r}$. The random vector of residuals was defined as $\mathbf{e_e}$. Birth year was fitted as a random environmental effect because husbandry and food was the same throughout the study and thus any year effects would represent random seasonal fluctuations in performance level. The (co)variance structure of the model fitted was:

$$V\begin{bmatrix}\mathbf{d}\\ \mathbf{m}\\ \mathbf{c}\\ \mathbf{r}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{A}\sigma_d^2 & 0 & 0 & 0 & 0\\ 0 & \mathbf{A}\sigma_m^2 & 0 & 0 & 0\\ 0 & 0 & \mathbf{I}_c\sigma_c^2 & 0 & 0\\ 0 & 0 & 0 & \mathbf{I}_r\sigma_r^2 & 0\\ 0 & 0 & 0 & 0 & \mathbf{I}_e\sigma_e^2\end{bmatrix} \qquad (11)$$

where $\mathbf{A}$ was the numerator relationship matrix, and $\mathbf{I}_c$, $\mathbf{I}_r$ and $\mathbf{I}_e$ were identity matrices of order equal to the number of litters, birth years and records, respectively, and σ_d^2, σ_m^2, σ_c^2, σ_r^2 and σ_e^2 were the direct additive, maternal additive, litter, birth year and residual variances, respectively. The covariance between the direct and maternal additive effect was set at zero. In Simm *et al.* (2002) the effect of this covariance component for growth traits was tested, using largely the same data, and found to be small and not significantly different from zero.

Model selection

The sufficient set of fixed and random terms to include in a mixed-model to adequately describe the accepted set of growth parameter values (A, B, Z and G_0) and live weight at 150 days of age (W_{150}) was based on analyses using an average information (AI) REML algorithm (ASReml; Gilmour *et al.*, 1995 and 1998). The convergence criterion for this algorithm was that the change in the log-likelihood value between iterations was less than 0·01. The calculations were done separately for each response variable.

The fixed effects considered were sex, birth type (single, twin or triplet), rearing type (single or twin) and age of the rearing dam (2, 3 or 4 years of age and older). An embryo transfer (ET) programme in 1992 and 1993 meant that in some cases a lamb was born and reared by a surrogate dam. The surrogate dam was always a Suffolk cross. The importance of a lamb having been natural born or from ET in combination with the breed of its rearing dam was also tested (the category levels were natural born lamb with 100% Suffolk dam or ET lamb with 75% or 50% Suffolk-rearing dam). The day of birth within a lambing season was included as a covariate. These main effects, their two-way interactions, and the covariate were included in the initial model. Animal (direct additive), birth year and residual were fitted as random effects.

The significance of each fixed term was determined by considering both the sequential and marginal F-statistic obtained from ASReml. Including the two-way interactions did not improve fit for any of the growth parameter values or W_{150} ($P > 0{\cdot}05$). For some growth parameter values, individual main effects were also unimportant ($P > 0{\cdot}05$). However, each main effect did define variation for at least one of the growth parameter values, and all were important when describing W_{150} ($P < 0{\cdot}05$). Therefore sex, birth and rearing type, the age and breed of the rearing dam, and the day of birth covariate were included as fixed terms in the mixed models fitted.

The random effects to be included in the model were selected by comparing log-likelihood values from a series of nested models (given the chosen set of fixed effects). The improvement in fit when adding a random term was assessed by comparing minus twice the difference in the maximum log-likelihood value (the log-likelihood ratio test) of nested models to a chi-square distribution with one degree of freedom. If the fit improved significantly ($P < 0{\cdot}05$) the random term was added to the model and the process continued until all random terms had been tested.

Model fitting

In the mixed models fitted, W_{150} and each growth parameter value (A, B, Z, G_0) were considered as the response variate. For such analyses one could presume that the growth parameter values were estimated with equal reliability for each animal. In practice, the s.e. of the estimates of these growth parameter values were expected to vary between

animals. This was partly because the number of observations per animal differed and partly because of the way these observations were distributed (variation in the frequency of recording at some ages). Both these sources of variation could be accounted for by weighted analyses using the reciprocal of the square of the s.e. of the estimate of the growth parameter value as the weight.

Weighted univariate ASReml analyses were therefore conducted for each growth parameter value. In these the across-animal residual variance (σ_e^2) is a weighted one. Since the weights themselves represented the uncertainty in the estimated parameter values for an animal, 'relative' weights were used which thus became scaled by the estimated σ_e^2.

As the ASReml software that we used did not allow a weighted multivariate animal model analysis to be carried out, only univariate analyses were done. However, the additive correlation between the growth parameter values and W_{150} was empirically estimated as the correlation between the corresponding estimated breeding values (EBVs). The EBVs were obtained as best linear unbiased predictions (BLUP) from the fit of the 'best' mixed model chosen for each growth parameter value and W_{150}.

We also wished to obtain the heritability (the ratio of additive genetic and phenotypic variance) for each growth parameter. Doing so required that the weighted residual variance ($\sigma_{e^2 wt}$) be adjusted to account for the weighting to allow calculation of the observed phenotypic variance (σ_p^2). This was done as

$$\sigma_f^2 = \sigma_{e^2 wt} / \Phi_{wt} \quad (12)$$

where σ_f^2 is the adjusted residual variance and Φ_{wt} is the median weight for each growth parameter. The median weight was used since the distribution of weights was skewed particularly for the estimates of mature size (A).

Comparison of selection and control line

One objective of the study was to compare the performance of the selection and control line. Least-squares means for BLUP EBV for W_{150}, A, B, Z, and G_0 were therefore obtained by fitting a simple fixed effects model (Genstat 5 Committee, 1998). The model included line, year and their interaction. Year, and its interaction with line, were fitted because differences between lines may have changed over time with selection.

Results

Estimation of the values of the growth parameters

The reasons for excluding sheep are shown in Table 2. The fewest sheep were retained with method IV, since some sheep were excluded because they lacked live weight records before weaning.

The mean values of the growth parameters were consistent across methods. Estimates of A were more variable than those of B which, in turn, were more variable than those of Z. Across methods, when the mean value of A was higher, the mean value of B was lower. As a consequence, the mean values of Z were more similar among methods (a coefficient of variation of the mean values of less than 2% rather than more than 5% for A and B).

The distributions of A were substantially skewed and highly kurtotic ($P < 0.001$). Although for some methods, the distribution of B and Z were also

Table 2 *Number of convergence failures and, of the remaining animals, number (percentage) of extreme growth parameters values obtained when using the five estimation methods*

Method	Failed to converge†	No. remaining	Criteria for rejection‡			No. used
			r.m.s. ≥ 3.5 kg‡	$A \geq 300$ kg	$Z \geq 2.4$	
Ia	42	1892	27 (1·4)	51 (2·7)	16 (0·8)	1818
Ib	33	1901	27 (1·4)	60 (3·2)	22 (1·2)	1818
II	109	1825	154 (8·4)§	85 (4·7)	28 (1·5)	1609
III	N/A	1934	N/A	108 (5·6)	54 (2·8)	1826
IV	89	1536	N/A	19 (1·2)	0 (0)	1517

† Analysis failed to converge (method Ia, Ib and II) or reached the boundary of search space (401 kg for method IV).

‡ An animal may be rejected on more than one criterion. For method III, the full record on 10 animals was rejected because $A < 20$ kg.

§ Number with r.m.s $\geq (\sqrt{3.5}/W_{\mu})^2 = 0.0028$, where $W_{\mu} = 35.4$ was the mean live weight of the 1934 animals considered in the study.

Table 3 *Mean correlation coefficient (standard deviation) of the growth parameters within and across sheep for each estimation method*

Correlation	Growth parameters	Method			
		I	II	III	IV
Within animals	*A, B*	−0·982 (0·009)	−0·976 (0·013)	−0·988 (0·005)†	N / A
	B, Z	−0·133 (0·666)	N / A	N / A	N / A
Across animals	*A, B*	−0·774	−0·791	−0·786	−0·793
	A, Z	0·609	0·642	0·535	0·663
	B, Z	−0·053	−0·117	−0·003	−0·161

† Correlation of B_0, the intercept of the regression of relative growth rate on $\log_e$ weight, and *B*.

asymmetrical, any disparity from normality was less severe.

The correlation between the *estimates* of the values of the growth parameters were investigated both within and across animals. These results are shown in Table 3. The 'within animal' correlation measures the extent of the association between *estimates* of pairs of parameters for an animal. For all methods, the within animal correlation of *A* and *B* was consistently very close to −1. The within animal correlation for *B* and *Z* was obtained only with method Ib and was small (−0·13) and variable (s.d. 0·67). Across animals, the findings were similar. The correlation of *A* and *B* (less than − 0·77) and of *A* and *Z* (greater than 0·54) remained high. Only the estimates of *B* and *Z* were relatively independent (correlation of −0·16 to −0·003).

The R-square values for the linear regression of estimated values of a growth parameter obtained from one method on that obtained from another were calculated (results not shown). In all cases, the regression coefficient was positive. The *R*-square values for *Z* were consistently the highest with correlation coefficients of 0·87 to 0·96.

Choice of method

Based on the results in Tables 2 and 3, and on properties of the distributions as discussed earlier, we chose to use the estimates of the growth parameters from methods Ia and Ib for further analysis because they resulted in (i) a large 'accepted set' of observations (1818 of the possible 1934 animals) and (ii) direct estimates of the lumped parameter *Z*, which itself had favourable properties (e.g. a low correlation with estimates of *B* both within and across animals).

Variance estimates

For the accepted set of growth parameter values from methods Ia and Ib the data consisted of 127 sires, 657 genetic dams and 815 rearing dams. Generally the genetic and rearing dam was the same animal; they differed when lambs were cross-fostered or were produced by embryo transfer. On average, a genetic dam lambed 1·7 times and gave birth to a litter of 1·8 lambs.

In Table 4, the log-likelihood values obtained during model selection are summarized for W_{150} and the growth parameter values. For presentation purposes, the log-likelihood is expressed as the difference from the value obtained from the most comprehensive model fitted. The 'best' model to describe W_{150} included a direct and maternal additive effect, as did that chosen by Simm *et al.* (2002) for analyses of similar data. A litter effect rather than a maternal additive effect defined variation in the growth parameters values ($P < 0·05$), with the exception of *Z* for which both maternal additive and litter variance was detected ($P < 0·01$).

The estimate of phenotypic variance and variance ratios obtained for W_{150} and *A*, *B*, *Z* and G_0 are shown in Table 5. The estimates for W_{150} were from an unweighted analysis whilst those for the growth parameter values are from weighted analyses. For the growth parameter values, the results are shown relative to the 'observed' phenotypic variance (adjusted as in equation 12).

For all measures, the direct heritability was at least moderate in size, with that for *Z* being high (0·72). This may be in part due to *Z* being defined as $A \cdot B$ and *A* and *B* having the high phenotypic correlation reported in Table 3. Although the mixed-model fitted was slightly different to that used by Simm *et al.* (2002) to analyse largely the same data, the estimates of direct (0·31 *v.* 0·29) and maternal (0·11 *v.* 0·16) heritability of W_{150} were similar in both analyses. The litter variance for G_0 was approximately twice that for the other growth parameters, which is likely to be reflecting its association with weight around birth.

Table 4 *Comparison of log-likelihood values for the various models fitted from univariate analyses of* W_{150} *(un-weighted) and the growth parameter values (weighted)*

Model fitted‡	Log-likelihood values†				
	W_{150}	A	B	Z	G_0
DR	11·60	5·10	10·10	30·38	41·80
DMR	**0·04**	2·90	10·10	3·93	26·00
DCR	9·69	**0·60**	**0·00**	3·93	**0·30**
DMCR	0	0	0	**0**	0

† Log-likelihood values expressed as the differences from the most comprehensive model fitted (DMCR). Values shown in bold identify the model that fitted 'best' for a measure.

‡ Random effects were defined as: D — direct additive; M — maternal additive; C — litter; R — birth year.

Univariate models alone were fitted in these analyses. However, an empirical estimate of the genetic relationship among the measures could be obtained as the simple correlation between their EBVs. The correlation between EBVs for mature size (A) and the rate parameter (B) was negative (–0·48), whilst the correlation between EBVs for mature size and the initial condition (G_0) and 150-day weight (W_{150}) were positive (0·39 and 0·54, respectively). The EBV for Z increased with EBVs for both A (0·56) and B (0·19).

Comparison of growth parameter values between sexes

The estimate of A was found to be 1·27 times as great for a male as for a female ($P < 0·01$; Table 6), which is similar to findings elsewhere (Hammond, 1932). This coincided with a greater maximum growth rate (0·480 kg/ day in males *versus* 0·379 kg/ day in females; $P < 0·001$). Although the rate parameter B in a male was 0·97 times that in a female, it did not differ between sexes ($P > 0·05$). The growth curves for the average male and female are shown in Figure 2.

Comparison of growth parameter values between lines

There was an interaction between line and birth year for EBV for W_{150} and the growth parameter values ($P < 0·001$). For W_{150}, A and Z the EBVs were always higher in the selection than in the control line, with the difference increasing over years. This is shown for the live-weight traits in Figure 3. In 1994, the final year of selection, the selection line was genetically 5·2 kg heavier in 150-day weight and 6·6 kg heavier in mature weight than the control line ($P < 0·001$). This coincided with a maximum growth rate in the selection line that was 1·12 times that of the control with mean values of 0·480 and 0·427 kg/ day, respectively.

The pattern of change in EBVs between lines for the rate parameter B was different. There was little differentiation between lines through 1991. Thereafter, the average EBV for B steadily decreased in the control line. In 1994 the mean value for the rate parameter was 0·01096 (s.e. 0·00005) in the selection line and 0·01016 (s.e. 0·00007) in the control line, an advantage of 8% to the selection line.

Table 5 *Estimate of the phenotypic variance* (σ_p^2)*, and ratios among variances (s.e.), for the 'best' model describing* W_{150} *(un-weighted) and the growth parameter values (weighted)*

	W_{150}	A	B	Z	G_0
σ_p^2	37·49	465·02	4·9353E-06	2·0323E-02	9·1154E-03
Ratio†					
h_d^2	0·313 (0·058)	0·365 (0·044)	0·384 (0·051)	0·722 (0·047)	0·554 (0·041)
h_m^2	0·108 (0·029)			0·055 (0·024)	
c^2		0·075 (0·027)	0·125 (0·031)	0·085 (0·024)	0·218 (0·030)
r^2	0·106 (0·050)	0·095 (0·047)	0·072 (0·041)	0·101 (0·049)	0·060 (0·034)

† $h_d^2 = \sigma_d^2/\sigma_p^2$, $h_m^2 = \sigma_m^2/\sigma_p^2$, $c^2 = \sigma_c^2/\sigma_p^2$ and $r^2 = \sigma_r^2/\sigma_p^2$, where σ_d^2, σ_m^2, σ_c^2 and σ_r^2 are the direct additive, maternal additive, litter, and birth year variances, respectively.

Table 6 *Least-squares means for W_{150} (live weight at 150 days of age) and for the estimates of growth parameter values (method Ia and Ib) by sex (1003 males; 786 females)*†

Sex	W_{150}	A	B	Z	G_0
Male	64·9	109·8	0·01 085	1·306	1·108
Female	54·5	86·3	0·011 22	1·030	1·028
Maximum s.e.‡	1·1***	3·8***	0·00039	0·030***	0·018***

† Weighted least-squares with the inverse of the squared s.e. of the estimated values of the growth parameters used as the weights.

‡ Asterisks indicate where, between sexes, estimated means differ.

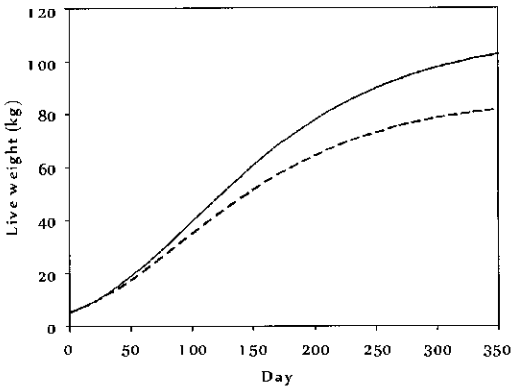

Figure 2 The estimated growth curve for the average male (——) and female (– – –) lamb.

Discussion

The way in which actual body weight changes with time in sheep, as with other animals, depends on the way in which they are treated in terms of their feeding and environment. Growth at a weight can also depend on health status. It is not sensible to expect data on actual growth, which may well be caused to depart from the potential because of deficiencies in feeding, environment and health, to be totally consistent with any particular form of growth function. Despite this being obvious the literature is full of examples where actual growth data, often of doubtful provenance, have been used to try to choose between growth functions. In clear distinction from this approach it has been found to be useful for several agricultural species (turkeys: Emmans, 1989; chickens: Gous *et al.*, 1999; pigs: Ferguson and Gous, 1993a and b; Knap, 2000; quail: Akbas and Yaylak, 2000; sheep: Friggens *et al.*, 1997; Zygoyiannis *et al.*, 1997) to use the idea of potential growth which can be described by a function. By definition this is the growth that would be observed in conditions that were not limiting. There is always a problem in saying that a particular set of conditions were not acting to limit growth, but there are often internal tests that can be used to see if this was likely to have been the case. One such test is to check that the values of the function using early and late growth data are consistent, as was done with method III in this work.

One strong attraction of the Gompertz function is that its two main parameters have meaning (A is mature size and B is a measure of the rate of maturing). For population mean data over a wide range of degree of maturity, the function is also easy to fit using non-linear regression. But as the size of the population providing the data decreases towards one so that, in the limit, they come from an individual animal, and as the range of weights becomes smaller, so the problems of estimation become greater. While the data from the great majority of our animals could be well fitted to the function with low residuals, and the values of its parameters estimated, the values of individual parameters could not be well estimated for a given animal. This was in part because the standard errors were appreciable but also because the estimates for A and B were highly correlated and hence were not independently estimated. The use of the lumped parameter Z, defined as $A \cdot B$, and where Z/e is the

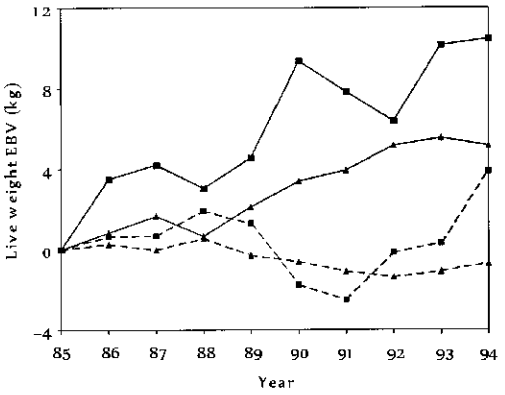

Figure 3 Genetic trends for 150-day (▲) and mature (■) live weight (kg) in the lean growth selection (——) and control (– – –) genotype.

maximum growth rate, helped. The value of the parameter Z was easier to estimate reliably for a single animal as it overcame, to some extent, the problem of the estimates of A and B being highly correlated.

The comparison of estimation methods was not based on a formal test. Since growth parameter values were obtained for the same set of animals for all methods, these estimates and their errors were not independent. Furthermore, the number of parameters fitted varied between methods as did the characteristics and amount of data considered (for instance individual weights *versus* relative growth rates). Even if the sets of growth parameter values were independent between methods, residual mean squares would in part reflect the unique features of the method. Any comparisons based on goodness-of-fit tests are unconvincing.

Instead, a more empirical approach was adopted to compare and choose between estimation methods. This involved considering the frequency with which an iterative fit converged and whether the estimates obtained fell within a defined and biologically sensible range for growth parameters (Table 2). As part of their criteria for choosing a non-linear function to describe growth in dairy cattle, Perotto *et al.* (1992) adopted a similar strategy. The attributes of the growth parameter values themselves were also considered. The within and between animal estimates of A and B proved to be highly and negatively correlated (Table 3) and, particularly for A, were skewed and leptokurtotic in their distribution. The estimate of the lumped parameter Z was comparatively independent of B and essentially normally distributed. Taken together, the non-linear fit of the Gompertz equation transformed to fit Z rather than A (method 1b) was the best and we chose it as the method to employ.

The mean values of A for the males and females of 109·8 and 86·3 kg (Table 6), can be compared with other estimates for Suffolk sheep. Oberbauer *et al.* (1994) reported the mature empty body weight in Suffolk males as 97·9 (s.e. 7·8) kg. This was based on the fit of the Brody growth equation to weights collected at 16 slaughter events spread between 1 and 600 days of age. Oberhauer *et al.* (1994) note that even at the final slaughter age, weight had not reached an asymptote since these animals were given food in a manner that allowed them to continue to fatten. While the form of the Brody equation is unsuitable, its use on these data is unlikely to cause any gross error in the estimate of the asymptote.

The ratio of the male to the female mature size observed in this study is close to that of 1·3 estimated by Hammond (1932). Between species the value of the rate parameter, B, is scaled to $A^{0.27}$ (Taylor, 1965 and 1980; Emmans, 1997). For the pre-weaning growth of eight mammalian species, including sheep, the value of the scaled rate parameter $B^* = B.A^{0.27}$, varied little around a mean of 0·03528 (Emmans, 1997). For the males and females in the current study, the values were 0·03858 and 0·03739 respectively, only a little higher than those expected on an interspecies basis.

While, in principle, an animal has values for A and B (and for G_0, but this is only the starting condition), and these reflect its inheritance to at least some extent, the difficulty of estimating these separate growth parameter values for an individual meant that the genetic analysis was not as straightforward as we had hoped. Since the frequency and spacing of live weight recording differed between animals, the reliability of our estimates of A and B varied between animals. Weighted analyses were used to account for this by fitting univariate mixed-models. Genetic covariances between the values of the growth parameters were therefore not obtained.

Mature size, A, and the rate parameter, B, were moderately heritable (0·37 and 0·38, respectively) as was live weight at 150 days of age (0·31). Effective selection to increase A and B therefore seems plausible. However, there appears to be an antagonism between the rate of maturing and mature size. Our empirical estimate of the genetic relationship between these growth parameters was substantially negative (–0·48). This suggests that the components of growth are inherently in balance, and disturbing this homeostasis may prove problematic. The persistence of the scaled rate parameter $B^* = B \cdot A^{0.27}$ across species is perhaps further evidence of this. Our lumped parameter $Z = A \cdot B$ was however highly heritable (0·72). Its higher heritability than either A or B probably reflects fewer problems with estimation; its higher heritability than weight for age probably reflects the greater amount of information used to estimate it. There is appreciable genetic variation in the overall means by which sheep grow, captured in Z, and this appears more amenable to selection.

After 9 years of selection on an index designed to increase lean growth rate, the index score of the selection line increased substantially by over 4 genetic s.d. units (Simm *et al.*, 2002). Although the index did not explicitly act to increase live weight *per se*, it did not constrain it to allow for more rapid improvement in lean growth. Consequences were

increases in live weight at 150-days (the age of selection), mature size and maximum growth rate as represented by Z.

The positive relationship between the EBVs for the growth traits observed in this study suggests such correlated selection responses should be expected. Where the absolute size or weight of an animal in addition to its lean composition is important, it is arguable whether such an increase in weight is in fact desirable. Examples of this are where there are limits in the carrying capacity of land (such as in marginal grazing areas) or where there is a desire for carcasses of given weight at given levels of fatness or conformation. A constraint on any increase in live weight may prove more sustainable in such situations, although undoubtedly would result in slower improvement in lean growth. The consequences of selection on correlated traits must be considered to ensure the outcome of a breeding programme is tailored to the economic and social demands of the industry to which it is applied.

Random regression is an increasingly popular tool to resolve the genetic merit of animals for records that are collected repeatedly over time (Schaeffer and Dekkers, 1994; Jamrozik and Schaeffer, 1997), such as the live weights in this study. In a companion paper, random regression methods have been used to analyse these same growth data, and the respective merits of the techniques compared (Lewis and Brotherstone, 2002).

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